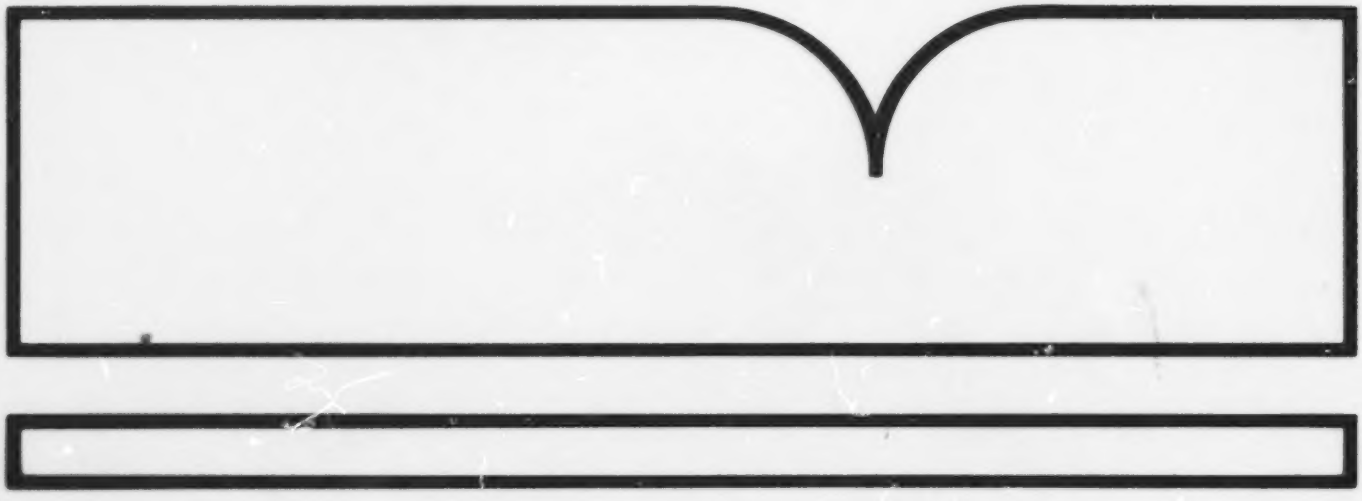
PB90-116633

Modeling Tree Level Processes

(U.S.) Corvallis Environmental Research Lab., OR

1989



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1. REPORT NO. EPA/600/D-89/164	2.
3.	PB90-116633
4. TITLE AND SUBTITLE: Modeling Tree Level Processes	5. REPORT DATE
	6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S): Cheryl Aeschbach Gay	8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS: NSI, ERL-Corvallis	10. PROGRAM ELEMENT NO.
	11. CONTRACT/GRANT NO.
12. SPONSORING AGENCY NAME AND ADDRESS: US Environmental Protection Agency Environmental Research Laboratory 200 SW 35th Street Corvallis, OR 97333	13. TYPE OF REPORT AND PERIOD COVERED: Symposium Paper
	14. SPONSORING AGENCY CODE: EPA/600/2
15. SUPPLEMENTARY NOTES: 1988 Proceedings of the 2nd US/USSR Symposium Air Pollution Effects on Vegetation, Sept. Raleigh, NC.	

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The foliar processes module is used as a reference point in the discussion, and is under development using the explanatory approach. The lower hierarchical level of processes, such as photosynthesis and nutrient allocation, is emphasized in simulation of the activities of the foliar organ. A branch growth module with which the foliar module will be coupled in the system, is also a process model, but is under development using the abstraction approach. A stand model, with which it will later be coupled, has been developed empirically, using the estimation approach. The development of modular simulators of sub-processes, utilizing various of the three developmental approaches, then coupling them is a robust approach to meeting information needs. The resultant aggregate models provide tools with the capabilities of incorporating current scientific knowledge to provide predictions which possess the characteristics of realism, generality and precision.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

REPRODUCED BY
U.S. DEPARTMENT OF COMMERCE
NATIONAL TECHNICAL INFORMATION SERVICE
SPRINGFIELD, VA. 22161

18. DISTRIBUTION STATEMENT: Release to Public	19. SECURITY CLASS (This Report): Unclassified	21. NO. OF PAGES: 28
	20. SECURITY CLASS (This page): Unclassified	22. PRICE

EPA Form 2220-1 (9-73)

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EPA/600/D-89/164

Title: MODELING TREE LEVEL PROCESSES

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For inclusion in :
Proceedings of the second US/USSR Symposium: Air pollution effects on vegetation
September 19-20, 1988
NC State University, Raleigh, North Carolina

Abstract

An overview of three main types of simulation approach (explanatory, abstraction, and estimation) is presented, along with a discussion of their capabilities limitations, and the steps required for their validation. A process model being developed through the Forest Response Program is used as an example. In construction of this tree process model, the various organs (such as foliage) are simulated using a modular plan of development.

The foliar processes module is used as a reference point in the discussion, and is under development using the explanatory approach. The lower hierarchical level of processes, such as photosynthesis and nutrient allocation, is emphasized in simulation of the activities of the foliar organ. A branch growth module with which the foliar module will be coupled in the system, is also a process model, but is under development using the abstraction approach. A stand model, with which it will later be coupled, has been developed empirically, using the estimation approach. The development of modular simulators of sub-processes, utilizing various of the three developmental approaches, then coupling them is a robust approach to meeting information needs. The resultant aggregate models provide tools with the capabilities of incorporating current scientific knowledge to provide predictions which possess the characteristics of realism, generality and precision.

Introduction

Simulation with mathematical models is an analytical tool whose use is becoming increasingly widespread. It is important that general concepts pertaining to modeling approaches and capabilities be realized and stated explicitly at the onset of any modeling activity. The objective of this paper is to place in perspective various aspects of process and empirical modeling, and how they relate to the modeling endeavors of the Forest Response Program (FRP) of the National Acid Precipitation Assessment Program.

The (FRP) has conducted a large research effort focused on determining the effects of acid precipitation on forest development. Research within the program has been conducted at varying levels of biological organization (Figure 1), ranging from seedling to regional scale. In order to structure this acquired information in a form which would aid understanding of the acid precipitation phenomenon, a conceptual whole-tree-physiology modeling system has been developed. The system will act as an explanatory interface between experimental information gained from seedling and branch studies, to aid in interpreting observations made at higher levels of stand and forest.

Systems can be modeled in a way that will either provide explanation, estimation, or abstract principles. The choice of a simulation objective, along with the nature of the observational information available for model construction, together determine the character of information obtained from the completed simulator. The level of biological organization for which observational data are available, compared with the desired level of prediction, also determines whether an empirical or process-modeling approach will be required. The term "empirical" pertains to models which are developed without direct reference to the biological processes involved. "Process" models, on the other hand, are derived by mathematical simulation of the underlying physical/chemical processes presumed responsible for the activity (activities) of interest.

The purpose of this paper is to identify some of the required steps in model development. These steps include defining performance criteria, verification techniques and validation processes. In addition, I will focus on the importance of defining the scope of a model. Since two general modeling approaches are commonly used, ie. empirical and process modeling, I will clarify the differences between them, and outline advantages and disadvantages of each. Finally, I will present and overview of a modeling system under development to

evaluate and predict tree responses to air pollution. This system is an aggregation of submodels utilizing elements from both empirical and process modeling approaches. Combining these techniques is one way of linking foliar processes to that of a tree, and tree growth processes to that of the stand.

Model scope

Before beginning any modeling activities, the researchers developing the model must clearly state what output is needed. Will there be predictions of size? activity? diversity? The type of information to be provided must be stated without ambiguity, prior to designing the model framework.

What entities will be of concern? In this discussion, emphasis is placed on describing trees - not leaves, forests, or stomata. What is the relationship of the model to the data supporting its development? Is the model output to be within the range of that data, and can thus be interpolated? Are there measurements of tree-level parameters, such as tree height and diameter or even whole-tree mass or total photosynthesis? Such a data bank would allow interpolation between measurements to provide tree-level output. In contrast, is the output outside the range of the database? Will it be necessary to extrapolate from what has been measured or observed, and go beyond the data to make other predictions. Answers to these questions define the scope of the model.

Model Assumptions

In stating the assumptions, all factors considered to have a significant effect on the behavior of the tree (variables and processes) are listed. The assumptions reveal the essence of the simplification of the physical system, and indicate how the model will represent tree behavior. If the goal is, as stated, to model the effect of pollutants on trees, the assumption will be made that particular pollutants (defined and listed) influence tree growth and functioning, affecting in some way the processes addressed in the model. The question arises then whether the mode of air pollution action on the physiology and growth is understood.

Another decision that must be made is the level of hierarchy. The level of hierarchy represents the level of biological organization, or complexity, to be modeled. Levels of hierarchy relevant to modeling forest processes , in decreasing ordr, would be forest-stand-tree-organ-cell, etc. In this example, the level of concern is the individual tree. Information may be utilized from lower levels, such as that of the organ (leaves, roots, stems, branches). One could also use information from progressively lower levels of organization - the cell level, the organelle level, or even the molecular level. Information from higher levels of organization (for example, the stand or region) will not be as directly useful in model development, but provides information characterizing constraints to system behavior. In this example, the behavior of the tree is simulated by aggregating sub-models simulating behaviors of various organs and physiological systems. The functioning of these organs and systems, in some of the sub-models, is represented by the behaviors of their particular subprocesses. In the foliar module, the lower hierarchical processes of ontogeny, nutrient cycling, and photosynthesis are represented.

Model Building: Steps, Performance, Verification and Validation

In forestry, seedlings are often used in experiments as surrogates for mature trees. How to make the link between the entity in which we are interested (tree, in this case) and the entity observed (seedling) is an unresolved issue. How can one go from studies on seedlings of the kind so frequently undertaken, to understanding effects on whole mature trees, or from seedlings to forests? How should the extrapolations be drawn? We can design experiments, we can test hypotheses on needles, on branches, but we still have difficulties in observing and understanding the whole tree, especially a large whole tree.

Modeling is a technique particularly suited to providing links between information at varying levels of biological complexity. In this case, the challenging link is from information taken from seedlings and laboratory studies, to inferences about whole trees and forests. To properly apply these modeling tools, a clear understanding of the different types of models is first needed, along with the types of information provided thorough their use. Basic strategies for simulation apropos of the creation of a model-based approach to tree level investigations, are reviewed here.

The process of modeling is often difficult to discuss. The difficulty arises not so much from its intellectual rigor, but rather from a failure to define clearly the relevant terms. Thus, one of my goals will be to focus on concise definition of terms. Modeling requires a simplification of processes and systems of processes, facilitating analysis of their behavior. The more complex the model, the more difficult the analysis of the represented system becomes. The first concern, therefore, in model development, is to try to maintain as much simplicity as possible. The ultimate utility of the model depends on successful simplification of the problem.

A typical sequence of activities associated with scientific research is outlined in Figure 2. The prelude is the creation of the proposal, followed by research and implementation. The proposal establishing a modeling effort would be expected to include

1) defining and bounding of the problem,
2) identification of goals and objectives,
3) citation of relevant data (whether it resides in the literature or will be gathered specifically for purposes of model development),
4) definition of performance criteria

I will use the Foliar sub-model of the whole-tree modeling system as an example. The objective of the development of this model is to characterize the effects of acid precipitation on foliar processes of a mature conifer. Lying within the bounds of the system are the various foliar processes which are most likely to show the influence of atmospheric pollutants, and external to the system are the environmental conditions, which act as input.

Performance criteria are the standards by which the model will be judged. The specification of performance criteria provides a measurable scale against which the success of the model will be judged. Before the onset of the modeling activity, the levels of precision required of the model must be defined. Establishing precision identifies the level of complexity that must be included, and helps to define the goal. The Foliar model will be expected to reflect the trends observed in experimental research on acid precipitation, and to provide that information to the other elements of the whole tree aggregate model so that the implications of these changes in foliar behavior on

whole tree growth may be explored. In this way, the Foliar model will act as an aid in interpreting those experimental results which may have appeared inconclusive.

Modeling research begins with construction of the working algorithm, which identifies the basic features of system operation. In this step, the elements of the system are defined, along with their state descriptors. The state variables when taken together, describe the status of the system. The questions addressed are:

What element is of concern?
How does it change?
What does it change to?
Where does it start?
Where does it move to?

In the Foliar model, the element of concern is the foliage (needles) present on the various branch segments of a branch extending from the main bole of a mature conifer. Of specific interest is its changing developmental status from first emergence to death and abscission from the branch. Foliar functions which reflect this changing status include growth, aging and senescence; nutrient dynamics; and net carbon production. The states of interest therefore include nutrient status, carbohydrate status, needle age and needle amount.

Interrelationships between the elements of concern and the states of those elements are defined, customarily by expression of the various mathematical relationships linking system elements. The algorithm is then converted into a formal modeling language. Forrester flow diagrams are common, followed by translation, through one of many computer languages, into executable code.

Model verification follows codification of the model. Sometimes this step is attained, yet unfortunately, it often is not. Model verification differs radically from model construction. Through verification, the simulated system behavior is compared with observations made in real life, and adjustments in the model are made where necessary. This calibration step provides the final opportunity to modify system organization before systems analysis and validation.

Systems Analysis is a systematic approach for defining the character of the simulator through an analysis of the internal interactions in the model. The goal is to define the consequences of variation in values of represented system states and rates, and predict resultant repercussions throughout the rest of the system.

Verification differs significantly from validation. Validation is the exercise of proving that the model is, in fact, true. It is fairly common knowledge in the world of science that a theory can never be proven true. The theory can, rather, only be proven false or fail to be invalidated. A model is an aggregation of theories and hypotheses. As the singular theory, the model can also never be proven true, but can only hold up under the tests made against it to date.

With planning, work, and luck, the process of model development reaches the implementation stage, and the work is finally put to use.

Empirical Models and Process Models

Two general methods are commonly used in modeling, the empirical- and the process- modeling technique. Both methods have strengths and weaknesses, and both are necessary for comprehensively addressing complex systems. Empirical modeling is an approach that is frequently used in forestry. Model output is at the same level as that of the data. In order to model a tree, tree-level information would be required. The field of forest science has a strong history of very effective empirical modeling [1,2].

In the process model, on the other hand, the outputs (or the predicted values) are at a higher level than the data. To construct a process model of trees, we would use information from the level of the organ (or perhaps an even lower level). A general rule of thumb in modeling is to avoid spanning more than three levels of hierarchy in a single model. The lower level would provide insight into system behaviors observed at the "intermediate" level. The highest level involved in the simulation reveals the impact of the simulated activities at the intermediate level. The success of an attempt to span a number of levels, such as an effort to model trees directly from the level of the organelle, for example, would be questionable.

The information embodied in functional relationships of the empirical and process models also differs [1]. The general form in which the ideal empirical model is expressed is

$$y = f(\text{measured factors, non-measured factors, measurement error}).$$

for a given response y. The form taken by the process model is

$$y = f(\text{measured factors, measurement error}),$$

with the assumption that all factors known to influence y significantly have been accounted for. The definition is very precise, here. All factors known to influence y significantly. The determination of significance is a subjective judgment. The implication is made that the system is well understood.

Characteristics of empirical models and process models are contrasted in Figure 3. The level of empiricism is lower than the level of prediction in the process model, whereas they coincide in the empirical approach. Empiricism is common in process models, but the role it plays is different than in the empirical model. The role of the lower level empiricism in the process model is to explain why a process occurs, rather than to predict what the process does. The level of empirical information is lower than the level of prediction.

Correlation between variables is characteristic of empirical models. One event has been observed to accompany another, whether or not the phenomena have a cause/effect relationship. Indeed, it has often been stated that correlation does not imply causality. In contrast, the process model emphasizes causality. What are the cause/effect relationships? A great deal of effort is spent determining ultimate causes of the system behavior. A number of changes have been measured in plant growth when the plants are exposed to pollutants. But are those changes causes or are they effects? It may be possible that a few cause/effect relationships, coupled with normal linking of feedback and regulatory systems within the plant would predict all of the changes that are observed.

Empirical modeling often utilizes a "top-down" viewpoint. A pattern emerges that is visible in overview. The process-approach is more typically

"bottom-up". Based on what is known about the processes in question, a simulator is constructed, and queried in an attempt to recreate observed behaviors. These trends are general, however, and it is possible to use either of the two perspectives in empirical or process-based approaches.

In empirical models, many of the approximations and the assumptions are hidden. They are imbedded somewhere in the error terms and in the coefficients. In a process model the attempt is made to make more of the approximations and assumptions explicit. It may be assumed that the plant is free from most stresses (such as those due to water or nutrient deficits, or stressful temperature conditions. Essentially, one assumes that the plant is in good shape apart from a factor that is out of the beneficial range.

It is interesting to note that similarly focused empirical and process models often initially provide the same information. However, a process model has greater potential for refinement and application to subsequent problems. As more is learned about the system, more detail can be included in the simulated processes. There is also a difference in what can be accomplished over time with each approach (Figure 4 [3]). Empirical models produce impressive results in a fairly short period of time, until the information content of the data set is fully exploited. A process model should provide an informational underpinning, providing the ability to go beyond the particulars of a given data set to general insights applicable more universally. The disadvantage is that initial progress appears much slower.

An empirical model usually arises from statistical analyses of observations taken at a given point place and time, and of given specific entities (in this case, trees). The tremendous variability in the genetic potential of plants to respond to various external factors has often been stated. There is variation in soil type. There is variation in climate. The empirical model can be difficult to surpass in re-creating observed behavior of particular trees at a given site, for the time frame for which data was collected. What happens when events occur which those trees have not previously experienced, when the genetic stock is varied, or when extrapolations are made beyond the range of previously observed responses?

Modeling Objectives and Approaches

Objectives and approaches to modeling differ, as described by Levins [4], and range can be expressed in a triangle [5] (Figure 5). Objectives range from representation of reality, to attainment of precision in prediction, to presentation of general principles. To achieve these objectives requires diversity in approach. Estimation approaches are used, for example, in the formulation of empirically based forestry yield models. The model represents observations that were made "somewhere" [6], identified at a point in time, and a place. Models arising from this approach incorporate reality and precision, and commonly attain a very impressive degree of precision, but lack generality.

A second approach is that of explanation. Examples of this type of model are the traditional process models. Explanatory models apply "everywhere and nowhere"[6], and are represented by models such as the mechanisms of photosynthesis and Mendel's laws of genetic inheritance. The models should apply everywhere, yet no one has observed those specific laws working infallibly in any one place. Reality is represented, with a degree of generality, but precision may suffer.

The third approach is abstraction, characterized by such methodology as that used in the study of theoretical population dynamics. The resulting models are precise, yet describe general trends in behavior; however, they may lack the ability to depict reality.

In brief, with a single approach, one may reasonably expect to achieve any two of these three kinds of objective but cannot expect to attain the third. It should be emphasized that the types of information available from a model depend on the modeling approach taken. A very real concern is that oftentimes information will be requested from models which were not designed to provide it, such as the use of explanatory models for the provision of quantitatively precise predictions. In such an instance, on the contrary, the other two approaches - abstraction and estimation - should be used, since they are designed to provide precise predictions.

The description of the validation process is always a challenge. Validation procedures and criteria differ for the three types of modeling approaches just mentioned, and are outlined in Figure 6. An empirical validation approach is suitable for validation of estimation models. The models are developed

dir tly from data. Their validity can also best be judged through agreement of their predictions with independent data. The precision of their predictions can be judged via the use of statistical methods designed for quantifying precision.

The abstract and explanatory models fall into the category of process models. The abstract model is developed independently of a particular set of data, or of reality. Since the interest is not in precision of representation of a set of data, the validity of these abstract models, is based instead on the correctness of the mathematical manipulations. Validation becomes more of a mathematical exercise. No particular data sets would be suitable, because all data contains various, unregulated compounding effects of genetics, environment, that may differ from place to place. For example, latitude is often a very important influential factor in plant response. If latitude is influential, but its effects are not included, data from various latitudes would be unsuitable for validation. One conclusion is that the results of the abstract model are also abstract. The worth of the abstract model is based on intellectual rigor. The predictions are consistent and plausible, yet are not expressed quantitatively, with predictable confidence intervals. They are not designed to provide that type of information.

Explanatory models, again are a type of process model. Data enter into explanatory models as supporting evidence, but are not employed directly in model formulation. Trends observed in the data are taken into account. The general observations that repeat time and again lend the shape to the processes being explained. The validity of these models is based on their general ability to interpret the observed phenomena, again not with precision, but with a consistent ability to predict trends. Validation is challenging, due to the question of how close is "close enough". The model may match trends, but a failure to account for all important trends may not be recognized. Observed discrepancies could arise from environmentally or genetically driven normal variation as well as from systematic shortcomings of the model. The model structure is based on logic and experimental evidence. The model can only be validated by its ability to generally track phenomena that have been observed.

It is important to note that a model need not be restricted to a single approach. Models which have been developed utilizing different modeling approaches may be, and often are, coupled. This coupling provides the capabilities to create aggregated models capable of displaying all three attributes

of reality, precision, and generality. King et al. [7] have described a general procedure for integration of process- and empirically-based models, useful in linking physiological and forest dynamics models.

An example

The topic of this paper is the modeling of whole-tree processes. The structure of the whole tree modeling system of the FRP can be seen in Figure 7. The major processes in the system are being addressed by a number of research groups within the FRP, with the individual processes divided along either disciplinary lines or spatial orientation. To facilitate modular development efforts, the numerous processes comprising the system have been carefully delineated, minimizing required interaction between modules.

The emphasis is to simulate the effect of pollutants on the growth and changing morphology of a tree. The effect of pollutants, however, is not at the tree level, but at the levels of the numerous sub-processes acting in concert to form the tree. Research in model development is focused on determining the process, or processes, that are directly impacted by the pollutants, or defining the first cause/effect relationships which are ultimately responsible for the effect of pollutants on tree development.

One module of the system, the Foliar submodel, as mapped out in Figure 8, will now be discussed in more detail.

The major working hypothesis in the foliar processes model is that normal foliar activities are modified by deposition of the mineral elements in acid precipitation, that are also used in normal needle function. Initial effects occur due to tissue damage and alteration of the efficiency of the processes such as photosynthesis and stomatal control (and ultimately respiration and transpiration). Ultimately, revision of the balances of these normally occurring foliar nutrients could reduce the efficiency of physiological processes, even without signs of visible damage.

The activities of foliage located on a given branch of a mature tree are under scrutiny. The states of interest in this subsystem include nutrient status, carbohydrate status, developmental age, and needle amount. The location on the tree, and its maturity are conditions of the environment of the branch which also influence the values of these state variables. Foliar functions which are

of major concern in the model include growth/maturation, photosynthesis/respiration, and nutrient reallocation (Figure 8). Although foliage is not limited to these activities, the mentioned processes encompass the major avenues of acid precipitation influence on foliage. These states and processes (and their interactions) define a simplified system encompassing the dominant pollutant responses. Water use through transpiration and evapo-transpiration will be assumed to be non-limiting, and is not addressed further.

Input to the system are environmental descriptors including weather and pollutant information. Supply of nutrients from the roots through the bole is input. Branch autonomy is assumed, providing a zero carbohydrate input. The Branch model supplies morphological information on the number of branch segments of each type (age cohort and their order).

Output from the system, will be net carbohydrate available for branch- and bole-wood growth and respiration. Information generated within the model are the values of the previously listed state variables. This net carbohydrate is the main contribution of the foliage to the rest of the tree, and as such, will be the input to other processes occurring on the tree.

Leaf area is calculated as a function of thermal time, and constants which characterize typical growth rates and maximal needle areas of typical branches. Increase in leaf area occurs during the expansion period of needle growth. Leaf mass/unit area changes dynamically with season and age. Total leaf weight is calculated by multiplying the area of a particular segment of needles, by its particular mass/unit area.

Tissue age plays a central role in the leaf model. "Age" represents physiological age, and is used as an indicator of tissue integrity. Age is calculated as a function of thermal time elapsed since needle emergence, and the expected life span of the needle tissue. At emergence of the needles, the tissue has an expected life span (in thermal time) characteristic of the species. Tissue age is predicted as a normalized value, and is the ratio of elapsed thermal time to the expected life span.

Needles grow in the spring, as described above. Carbohydrate is fixed via photosynthesis during the summer growing season. During autumn, additional branch thickening takes place (as simulated in the branch growth model). If

insufficient branch wood is incremented to support the foliage present on the branch (determined in the branch growth sub-model), loss of the excess foliage is then predicted to occur late in the season.

Tissue nutrient concentration is governed by the rates of input and outflow from the needles. Input of mineral nutrients is from root uptake and reallocation from older foliar cohorts. Root uptake is not simulated within this model, but is accepted as input. A balanced, ample supply of nutrients from the roots is assumed, so the variable quantity determining source strength is the changing quantities of aging needles.

The rate of nutrient retranslocation is a function of relative sink and source strengths. The sink is the newly expanding foliage, and the sources are the soil and the adjacent older foliage. Nutrient loss from a foliage cohort is through reallocation to a younger needle cohort, and leaching. Nutrient movement through reallocation to the younger foliage is governed by season change.

Nutrient leaching is a function of cuticular resistance, rain amount, and the ion concentration gradient between foliage and rain.

A number of excellent photosynthesis models are already in existence. They range in degrees of complexity and aggregation. Two models of conifer gas exchange have been developed by Lohammar et al. (1980) specifically to provide a suitable biological background for the modeling of plant growth. One model is complex, and operates on a 5-minute time step, while the simplified model operates on a daily basis. The simpler version will be employed to provide photosynthetic calculations required in the Foliar processes model, providing estimates of daily net photosynthesis, transpiration rate, and water potential.

Photosynthetic capacity declines with leaf age, and in many cases reflects a reallocation of nitrogen [8]. Photosynthetic capacity in the model is therefore governed by leaf age and nitrogen concentration.

Like the concentrations of mineral elements, foliar supplies of carbon also change over the growing season. A within-leaf storage pool of labile carbohydrates contains carbohydrate that is not used immediately in growth. The rate of movement of this stored carbohydrate is a function of season, which governs the movement between foliage and other tree organs (roots, branch and bole meristems).

In the Foliar model, emphasis is placed on the simulation of chronic damage by atmospheric pollutants, where foliar activities are hampered, rather than irreversibly and radically altered. Simulation of the complications of damage due to more severe disruption are beyond the scope of the model.

Changes in net carbohydrate production induced by pollution are modeled in two ways, one immediate and the other long-term. Immediately, atmospheric pollution decreases the photosynthetic efficiency of the foliage for the day of pollution exposure. Exposures to chronic levels of pollution decrease the life expectancy of the tissue. The result of this decreased life expectancy are that the leaf tissue ages more rapidly. Leaf aging, in turn, is associated with lowered photosynthetic capacities.

The effect of acid rain on cuticle function is also simulated as an acceleration of the aging process, similar to the method used for chronic air pollution effects on tissue maturity. With increased age, retention of moisture on the leaf increases, representative of increased surface roughness. As the cuticle ages, it also provides lower resistance to leaching, thus resulting in greater rain-induced nutrient loss.

In conclusion

A common basic assumption in tree simulation is that of the maintenance of a particular allometric structure. Maintenance of a particular allometry may help to constrain model predictions to those behaviors most typically observed. However, the constraining effects of fixed allometry may prove to be a serious downfall in predicting the effects of environmental changes. Environmental stresses can affect the trees in such a way as to disturb their generally-observed regular structure. This realization requires the formulation of a more mechanistic approach to the regulation of morphology. The linking of a model simulating changes in foliar status to the model of branch morphology as described above, is a step toward determining the cause-effect nature of evolution of tree form.

The Foliar processes submodel will also serve to extend a model simulating stand-level processes. In this role, foliage is be addressed at the canopy level, rather than a single branch. Because of their empirical background,

stand models embody the attributes of reality and precision. Numerous empirically-derived stand models are in existence that have a history of satisfactory performance.

In the FRP's regulatory objectives, a reasonable level of precision is required. However, predictions will be made for responses of trees to air pollution which are expected to occur outside the range of the environmental conditions from which most stand models have been developed. This predictive proficiency demands the capabilities of generality, which are outside the strengths of estimation models. The addition of the process-level foliar subcomponent to the empirical stand model should extend the stand model's capabilities to include generality. This union of the two methodologies should fortify the reliability of the stand model in these unknown conditions, and provide for defensible extrapolations beyond the range of the data from which the original stand model was derived.

These various model components, have been developed utilizing various of the three developmental approaches. Coupling them is a robust approach to meeting information needs. The aggregate models utilize the particular strengths associated with the approaches used to assemble the parts, and provide tools with the capabilities of incorporating current scientific knowledge to provide predictions which possess the characteristics of realism, generality and precision.

Acknowledgments

I would like to thank Dr. Dominique Bachelet, Dr. William G. Warren, and Dr. William E. Winner for valuable comments.

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Figures

Figure 1. Levels of organization at which research is conducted in the Forest Response Program.

Figure 2. Procedural steps in a research program, and their sequence of execution.

Figure 3. Contrasting characteristics of empirical and process models.

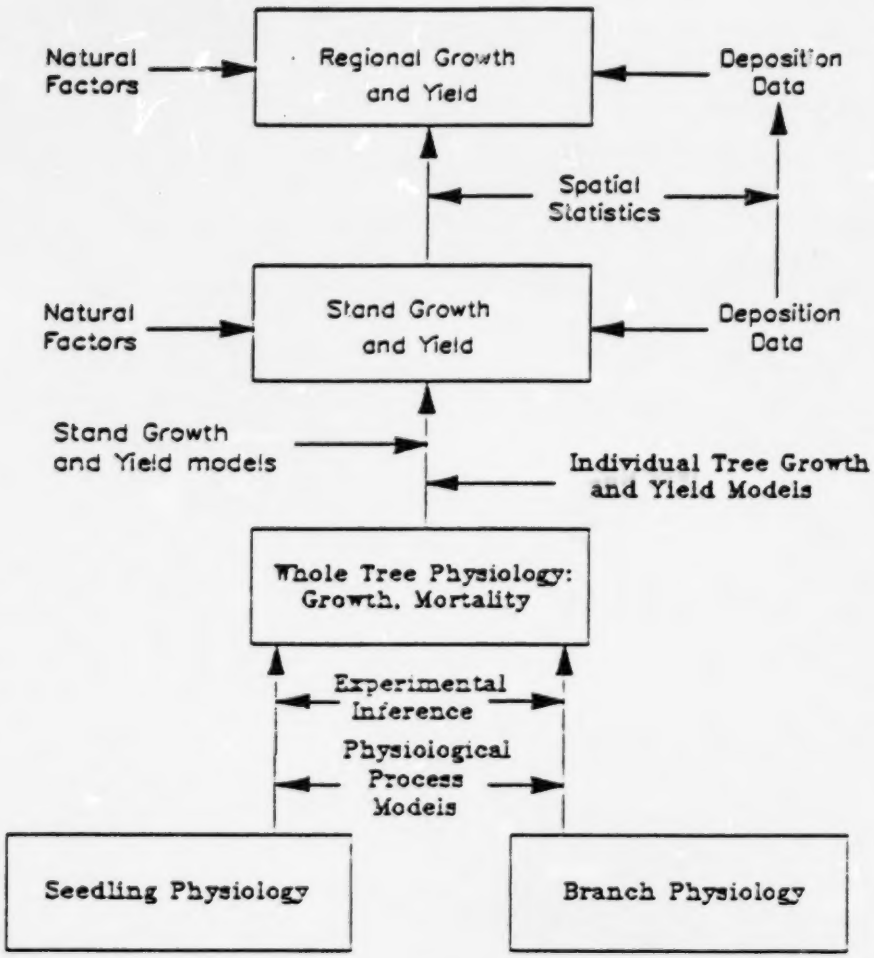
Figure 4. Perceived progress over time in process and empirical models.

Figure 5. Objectives and approaches to modeling, with examples of each type.

Figure 6. Validation criteria and procedures for the three types of modeling approaches.

Figure 7. Schematic of a whole tree model under development to address the impact of atmospheric pollution.

Figure 8. Diagram of processes addressed in a model of foliar processes designed to address pollution response.



FRP Levels of Organization

PROPOSAL

- Definition and bounding of problem
- Identification of goals and objectives
- Conceptual modeling
- Data acquisition
- Definition of performance criteria

RESEARCH

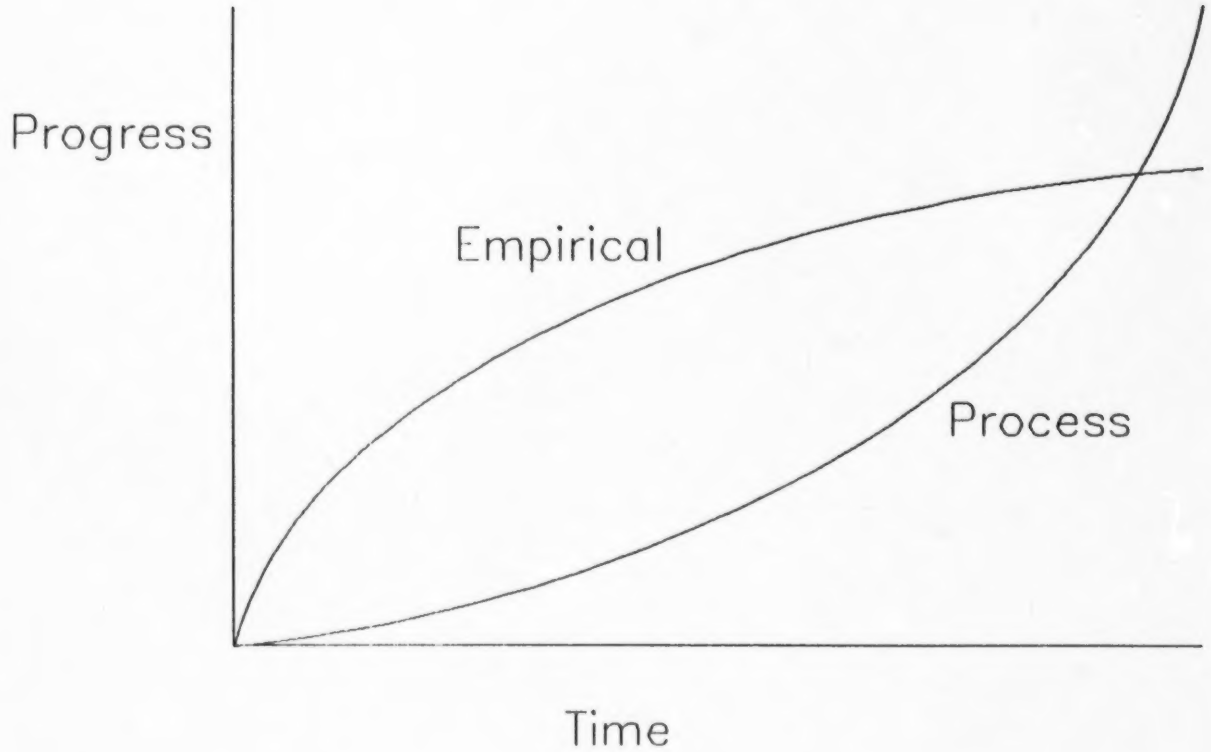
- Construction of working algorithm – identify:
  - Relevant elements and states
  - Interrelationships between elements and states
  - Mathematical relationships
- Conversion of algorithm into formal modeling language
- Model verification
- Systems analysis

IMPLEMENTATION

Empirical model	Process (mechanistic) model
– levels of prediction and empiricism coincide	– level of empiricism lower than level of prediction
– correlation between variables represented	– causality between variables explicitly represented
"Top–down"	"Bottom–up"
– many approximations & assumptions hidden	– many more approximations & assumptions explicit

-- initial information content may be no different --

– greater potential for improvement

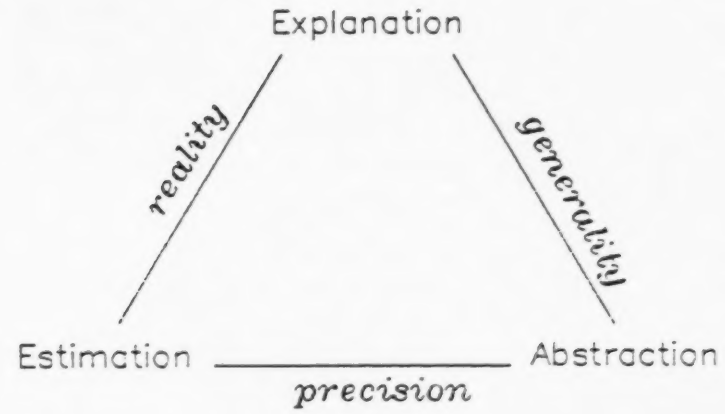

Progress
Empirical
Process
Time

Modeling *objectives*
and approaches

Photosynthesis

Mendels laws of genetic inheritance

"everywhere and nowhere"

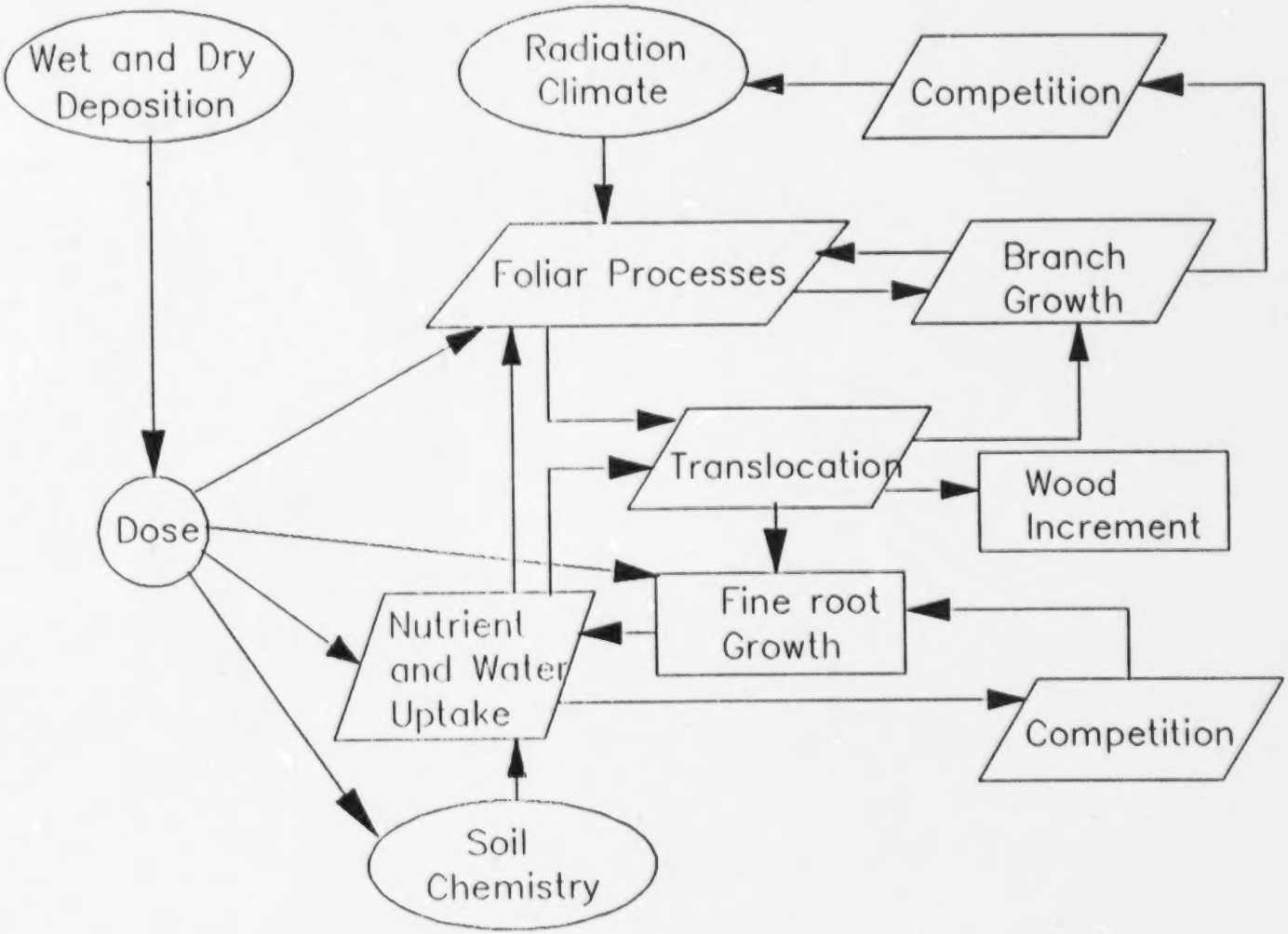


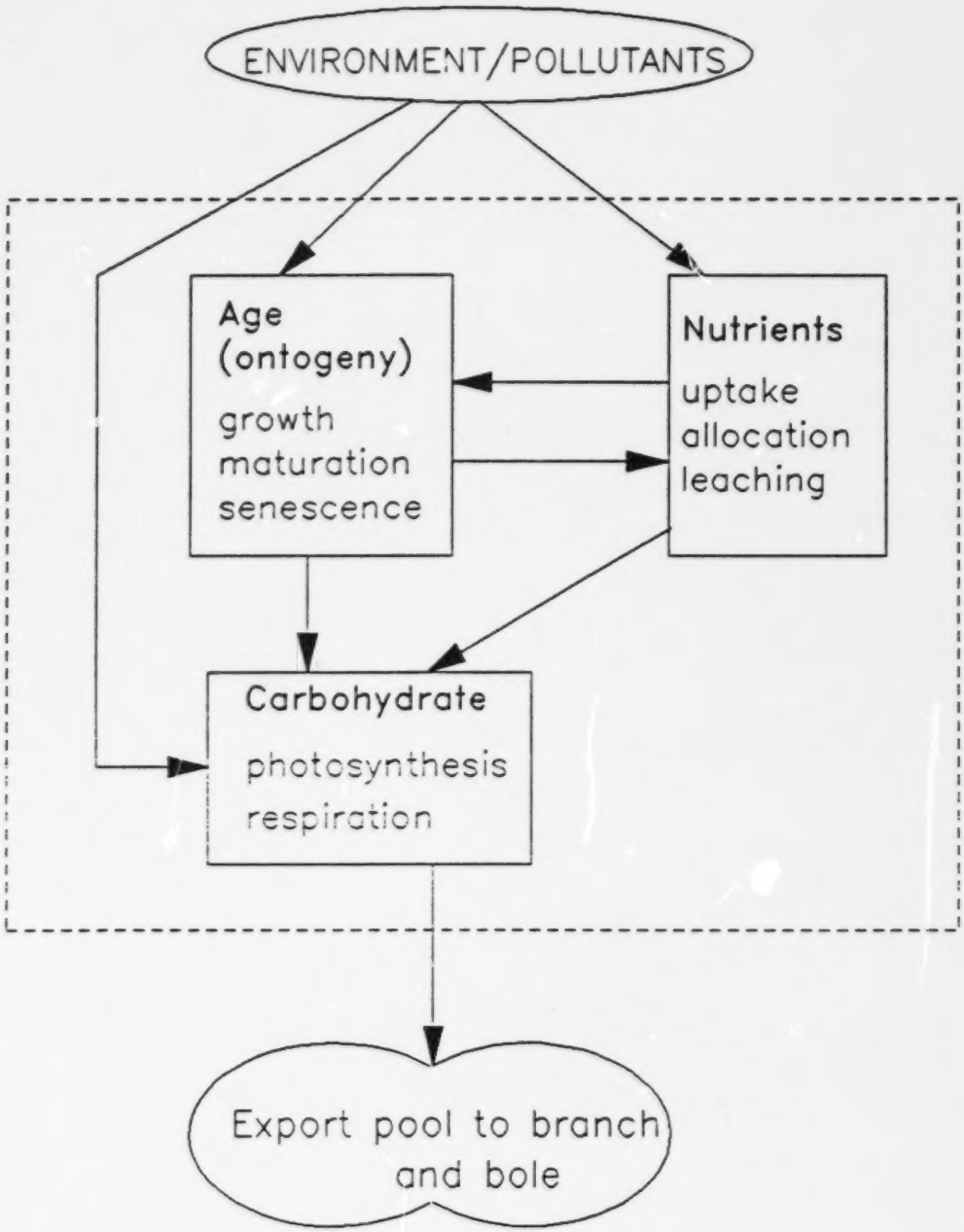
Forestry yield models

"somewhere"

Theoretical population dynamics

Empirical	Process	
Estimation models	Abstract models	Explanatory models
– developed directly from data	– independent of data	– generic concepts based on supporting evidence
– validity based on agreement with independent data	– validity based on correctness of mathematical manipulations used to develop final equation set	– validity based on their ability to interpret observed phenomena in terms of cause–effect relationships
		– challenging to validate
– judged on basis of statistical precision	– judged on basis of intellectual rigor consistency	– judged on basis of logic experimental evidence


Wet and Dry Deposition
Radiation Climate
Competition
Foliar Processes
Branch Growth
Translocation
Wood Increment
Dose
Fine root Growth
Nutrient and Water Uptake
Competition
Soil Chemistry


ENVIRONMENT/POLLUTANTS
Age
(ontogeny)
growth
maturation
senescence
Nutrients
uptake
allocation
leaching
Carbohydrate
photosynthesis
respiration
Export pool to branch
and bole